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SHORTER ARTICLES AND DISCUSSION

STUDIES ON INBREEDING—IV

ON A GENERAL FORMULA FOR THE CONSTITUTION OF THE nTH GENERATION OF A MENDELIAN POPULATION IN WHICH ALL MATINGS ARE OF BROTHER × SISTER[1]

I. IN a former paper in this series[2] the constitution of a Mendelian population in which all mating was of the brother × sister type was worked out empirically. The results there presented may be put in the form of a general formula, by means of which the constitution of any generation may be written down from a knowledge of the preceding generation; that is from a knowledge of the $n - 1$th generation the nth generation may be at once written down.

II. This general formula may be developed as follows. A single character pair will be considered, A denoting the dominant character and a the recessive. Equal fertility for all matings is assumed, the number of individuals per family being taken as $2s$, of which s are males and s are females. One family will then make s matings and produce s families in the next generation. Each mating is, by hypothesis, of a brother with his sister.

Starting as before with a pair from a population in which all individuals are of constitution Aa there will be in the next generation one family of the $AA + Aa + aA + aa$ type. In all succeeding generations there will be six types of families, viz.:

(1) AA families.
(2) $AA + Aa$ families.
(3) Aa families.
(4) $Aa + 2Aa + aa$ families.
(5) $Aa + aa$ families.
(6) aa families.

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[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 66.

It seems desirable to publish as a general series of "Studies on Inbreeding" the results of certain investigations now in progress in this laboratory. The three papers which have already appeared in this series, without the general title, are: 1. "A Contribution towards an Analysis of the Problem of Inbreeding," AMER. NAT., Vol. XLVII, pp. 577–615, 1913. II. "Tables for Calculating Coefficients of Inbreeding," Ann. Rept. Me. Agr. Expt. Sta. for 1913, pp. 191–202. III. "On the Results of Inbreeding a Mendelian Population: A Correction and Extension of Previous Conclusions," AMER. NAT., Vol. XLVIII, pp. 57–62, 1914.

[2] AMER. NAT., Vol. XVLIII, pp. 57–62, 1914.

The proportionate number of each of these types of families will change in successive generations according to the following system.

Let o_{n-1} denote the number of AA families in the $n-1$th generation, and
p_{n-1} denote the number of $AA+Aa$ families in the $n-1$th generation, and
q_{n-1} denote the number of Aa families in the $n-1$th generation, and
r_{n-1} denote the number of AA and $2Aa$ and aa families in the $n-1$th generation, and
u_{n-1} denote the number of $Aa+aa$ families, and
v_{n-1} denote the number of aa families.

It will be possible to write down u and v in any case without calculation because of the symmetrical relations of a Mendelian population, since always under normal conditions such as are assumed in the general treatment, we have

$$\begin{aligned} u_{n-1} &= p_{n-1}, \\ v_{n-1} &= o_{n-1}, \\ u_n &= p_n, \\ v_n &= o_n. \end{aligned}$$

It is necessary, therefore, to consider only the coefficients for the first four types of family. In the nth generation the constitution of the population in respect of *families* (not individuals) will be as follows:

Families in nth generation

$$\begin{aligned} &= s(o_{n-1} + 1/4p_{n-1} + 1/16r_{n-1})AA \text{ families} \\ &\quad + s(1/2p_{n-1} + 1/4r_{n-1})AA + Aa \text{ families} \\ &\quad + s(1/8r_{n-1})Aa \text{ families} \\ &\quad + s(1/2p_{n-1} + q_{n-1} + 1/4r_{n-1})AA \\ &\qquad + 2Aa + aa \text{ families} \\ &\quad + s(u_n)Aa + aa \text{ families} \\ &\quad + s(v_n)aa \text{ families.} \end{aligned}$$

Or, taking coefficients alone we have

$$\begin{aligned} o_n &= o_{n-1} + 1/4p_{n-1} + 1/16r_{n-1}, \\ p_n &= 1/2p_{n-1} + 1/4r_{n-1}, \\ q_n &= 1/8r_{n-1}, \\ r_n &= 1/2p_{n-1} + q_{n-1} + 1/4r_{n-1}, \\ u_n &= 1/2u_{n-1} + 1/4r_{n-1} = p_n, \\ v_n &= v_{n-1} + 1/4u_{n-1} + 1/16r_{n-1} = o_n. \end{aligned} \qquad \text{(i)}$$

III. Let us see how this formula works out in a concrete case. Assume the same conditions of fertility as in the former paper, that is, put $2s=32$, or $s=16$. Start with a single $AA+2Aa+aa$ family.

Then

$$\begin{aligned} o_{n-1}&=0,\\ p_{n-1}&=0,\\ q_{n-1}&=0,\\ r_{n-1}&=1. \end{aligned}$$

Then in the next generation we shall have

$16\{0+1/4(0)+1/16(1)\}=1\mathrm{AA}$ family
$+16\{1/2(0)+1/4(1)\}=4(AA+Aa)$ families
$+16\{1/8(1)\}=2Aa$ families
$+16\{1/2(0)+0+1/4(1)\}=4(AA+2Aa+aa)$ families
$+4(Aa+aa)$ families
$+1aa$ family.

This is the fact.

In the next generation we shall have

$16\{1+1+1/16(4)\}=36AA$ families
$+16\{1/2(4)+1/4(4)\}=48(AA+Aa)$ families
$+16\{1/8(4)\}=8Aa$ families
$+16\{1/2(4)+2+1/4(4)\}=80(AA+2Aa+aa)$ families
$+48(Aa+aa)$ families
$+36(aa)$ families.

This is the fact.

In the next generation we shall have

$16\{36+1/4(48)+1/16(80)\}=16\times 53=848AA$ families
$+16\{1/2(48)+1/4(80)\}=16\times 44=704(AA+Aa)$ families
$+16\{1/8(80)\}=160Aa$ families
$+16\{1/2(48)+8+1/4(80)\}=16\times 52=832(AA+2Aa+aa)$ families
$+704(Aa+aa)$ families
$+848aa$ families.

Succeeding generations follow the same law and need not be worked out in detail.

IV. So far the discussion has confined itself to families, as this must be the basic unit in the theory of any form of inbreeding. Turning to individuals we have the following simple relations to pass to individuals.

In the nth generation the number of

AA (or aa) individuals $= 2s(o_n) + s(p_n) + 1/2s(r_n)$,
Aa (or aA) individuals $= 2s(q_n) + s(1/2p_n) + 1/2s(r_n)$.

The first of the above expressions multiplied by 2 gives the total homozygotes, and the second multiplied by 2 gives the total heterozygotes.

RAYMOND PEARL

PARALLEL MUTATIONS IN ŒNOTHERA BIENNIS L.

IN the summer of 1912 I cultivated pure strains of *O. biennis* L. and of the *O. biennis cruciata* de Vr. of our Dutch dunes, as well as of their hybrids, made with the purpose of studying the behavior of the *cruciata*-character in crosses. In one of these cultures I unexpectedly obtained two mutants, which because of their similarity to corresponding variants derived from *O. Lamarckiana* have been called *O. biennis nanella* and *O. biennis semi-gigas.* The first mutant, *O. biennis nanella,* occurred in the second generation of the cross *O. biennis* × *O. biennis cruciata* and differed from *O. biennis* in all those points which separate *O. Lamarckiana nanella* from *O. Lamarckiana.* The other variant, *O. biennis semi-gigas,* appeared in the second generation of the reciprocal cross, *O. biennis cruciata* × *O. biennis,* suggesting immediately by its much more vigorous habit and especially by the larger size of its buds and flowers the differences between *O. Lamarckiana* and *O. gigas.* A count of its diploid number of chromosomes proved it to deserve the name *semi-gigas,* 21 chromosomes being shown by nuclear plate-stages in the meristematic tissue of young buds. From these facts, showing that *O. biennis* is in a mutating condition, I drew the conclusion that the phenomenon of mutation in the genus *Œnothera* is older than the species *O. Lamarckiana*—*O. biennis* generally being considered to be an older species than *O. Lamarckiana*—and further, that the mutations in this group can not be the result of hybridization, as was assumed by some authors at that time—nobody doubting of the purity and constancy of *O. biennis.* As a matter of fact, both of my mutants have been derived from crosses between *O. biennis* and *O. biennis cruciata.* But I laid special emphasis on the fact that *O. biennis* and *O. biennis cruciata* have exactly the same germinal constitution except for the factors that determine the shape of the petals, *O. biennis cruciata* being prob-